

COMPARATIVE HABITAT UTILIZATION BY ESTUARINE MACROFAUNA WITHIN THE MANGROVE ECOSYSTEM OF ROOKERY BAY, FLORIDA

Peter F. Sheridan

ABSTRACT

Abundance and biomass of juvenile and adult decapods and fishes in adjacent intertidal mangrove, seagrass, and open water habitats were compared using a quantitative drop sampler. Replicate samples were taken in each habitat in July, September and December 1988 and April 1989. Over all samples, fish densities were higher in non-vegetated, open waters (74% of the total caught) than in flooded red mangrove (*Rhizophora mangle*) prop roots or mixed seagrass beds (13% each). Spotfin mojarra (*Eucinostomus argenteus*) was the dominant fish collected among prop roots, yellowfin menhaden (*Brevoortia smithi*), scaled sardine (*Harengula jaguana*), and striped anchovy (*Anchoa hepsetus*) were most abundant in open waters, and bay anchovy (*A. mitchilli*) dominated the catch over seagrasses, although there were seasonal changes in dominant species. Shrimp densities were higher in seagrass habitats (74% of the total captured) than in open waters (22%) or among mangrove prop roots (4%). Habitat dominants were longtail grass shrimp (*Periclimenes longicaudatus*) and pink shrimp (*Penaeus duorarum*) in seagrasses, American grass shrimp (*P. americanus*) in open waters, and Florida grass shrimp (*Palaemon floridanus*) among mangrove prop roots. Over all samples, crab densities were higher in seagrass habitats (47% of those collected) than in open waters (33%) or mangroves (20%). Habitat dominants were blue crab (*Callinectes sapidus*), iridescent swimming crab (*Portunus gibbesii*), and redhair swimming crab (*Portunus ordwayi*) among seagrasses, green porcelain crab (*Petrolisthes armatus*) and flatback mud crab (*Eurypanopeus depressus*) in open waters, and broadback mud crab (*Eurytium limosum*) in flooded mangroves. On a monthly basis, among-habitat differences in density or biomass of major taxa did not exhibit any patterns, with the exception of shrimp which were always significantly more numerous in seagrasses than in one or both alternate habitats. Flooded red mangroves were, at times, utilized by both resident and transient fishes and crabs (but not by shrimps) at densities similar to those in seagrasses and open waters.

Mangroves are the dominant vegetation of low energy shorelines in the tropics and subtropics (Chapman, 1977). The only permanent mangrove habitat in the continental United States is found in Florida (Sherrod and McMillan, 1985), where mangrove acreage is almost twice as extensive as emergent tidal marsh vegetation (Lewis et al., 1985). The importance of emergent and submerged vegetation to marine and estuarine species of commercial and recreational value has been known in a correlative sense for many years (Martosubroto and Naamin, 1977; Turner, 1977; Odum et al., 1982; Zieman, 1982). However, quantitative aspects of habitat use and function of coastal ecosystems have been addressed only recently. For example, Thayer et al. (1987) recorded average fish densities among red mangrove (*Rhizophora mangle*) prop roots similar to densities found by Sogard et al. (1987) in seagrasses (*Thalassia testudinum* and *Halodule wrightii*). Zimmerman and Minello (1984) have shown that juvenile brown shrimp (*Penaeus aztecus*) and blue crab (*Callinectes sapidus*) were significantly more abundant in flooded smooth cordgrass (*Spartina alterniflora*) habitat than in adjacent non-vegetated waters. Heck and Thoman (1984) collected greater numbers of blue crab and grass shrimps (*Palaemonetes* spp.) from high salinity eelgrass (*Zostera marina*) beds than from non-vegetated waters. However, Heck and Thoman (1984) did not observe this relationship in low salinity shoalgrass (*Halodule wrightii*) beds, and fishes appeared equally abundant in both habitats regardless of location. Compared to non-veg-

etated waters, vegetated habitats may provide a greater degree of food or refuge from predators or both (Heck and Thoman, 1981; Minello and Zimmerman, 1983, 1985; Wilson et al., 1987; Rozas and Odum, 1987; Wilson, 1989).

The mangrove ecosystem of southern Florida, encompassing adjacent mangrove roots, seagrasses, and open waters, supports a variety of commercial and recreational fisheries (Tilmant, 1989). Faunal utilization of intertidal mangrove habitats is relatively unstudied, and comparison of fish and decapod densities among mangrove prop roots with densities in alternate, nearby habitats has not been addressed. The objective of this study was to quantify and compare densities of mobile macrofauna among adjacent intertidal red mangrove prop roots, seagrass beds, and non-vegetated waters in Rookery Bay, Florida.

METHODS

Area Description.—Located in Collier County near Naples, Florida, the Rookery Bay National Estuarine Research Reserve covers 3,400 ha of mangrove-dominated habitat (47% of the area is mangroves). It is composed primarily of red mangrove but also contains black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*) (Rookery Bay National Estuarine Research Reserve, 1986). The research reserve also contains seagrass meadows, primarily of shoal grass and secondarily of manatee grass (*Syringodium filiforme*), star grass (*Halophila englemanni*), and turtle grass (*Thalassia testudinum*), that cover an estimated 20% of the open bay floor (Yokel, 1975). Salinities are stable and usually exceed 30‰ except after heavy rains during August–September that can drive salinities down to nearly 0‰ for short periods, followed by recovery to high salinities within 1–2 months (Yokel, 1975). Sampling sites were located in northern Johnson Bay along the southern edge of the research reserve (26°01'N, 81°44'W).

Experimental Design and Sampling Methods.—Densities of fishes and decapods among flooded red mangrove prop root, seagrass, and open water habitats were compared using quantitative drop sampling (Zimmerman et al., 1984). Samples were collected in July, September, and December 1988 and April 1989 during spring tides. A preliminary survey in June 1988 located and prepared 10 prop root sampling areas (fixed sites for repetitive sampling) and marked adjacent seagrass beds and open waters (non-fixed sites for haphazard sampling). Mangrove sites were fixed because they had to be prepared in advance and impacts to these protected species had to be minimized. Photographs taken over the sampling period did not reveal any stress to the mangroves. Seagrass and open water sites were not fixed because drop sampling disturbs soft sediments (e.g., leaving deep footprints). Mangrove sites were 1.5–1.7 m diameter expanses of prop roots (the circular drop sampler was 1.8-m in diameter) between tree trunks, along the edge of the mangrove forest, with maximum water depths of 1 m. To allow positioning of the drop sampler, a 0.5-m wide path was cleared around each perimeter by cutting prop roots to the sediment surface. Canopies at each site were generally high enough to permit access of the drop sampler, but a few overhanging limbs were removed with presumed minor impacts to the shade component of the natural canopy. Adjacent seagrass and open water sites (maximum depths of 1 m) needed no site preparation.

For collections, the drop sampler was hoisted on a boom mounted on the bow of a skiff and maneuvered quietly over the sampling site. The sampler was then dropped to the substrate and subsequently pushed 15–20 cm into the substrate to seal off the sample. Prior to disturbing the sample surface, minimum and maximum water depths were measured and a 10-cm diameter core was taken to a depth of 10 cm to characterize submerged vegetation. Most of the water enclosed by the sampler was then pumped through a 1-mm mesh plankton net. The remaining water was thoroughly swept with dipnets where possible (any animals collected were placed in the plankton net) then pumped out. Organisms visible on the surface were removed and placed into the cod end of the plankton net, which was then detached and preserved first in 10% formalin–seawater and later in 70% ethanol. Laboratory processing included identification, counting, and measuring of fishes and decapods (standard length of fishes, total length of shrimps, carapace width of crabs). Common names for organisms follow Robins et al. (1980) and Williams et al. (1988). Some specimens could not be identified with certainty beyond the family or generic level usually due to small size and damage during collection or preservation. Randomized subsamples of up to 25 individuals were measured if large numbers were collected. Organisms in each sample were then grouped into major taxa (fishes, shrimps, crabs), blotted dry and weighed to estimate biomass. Crab biomasses were underestimated due to typical leg loss upon preservation.

Drop sampler efficiency was reported by Zimmerman et al. (1984) as 94% recapture of marked penaeid shrimp from emergent marsh and open water habitats. My own unpublished tests from other

studies indicate recapture rates over all taxa of 82% in seagrasses, 94% in emergent marshes, and 88% in open waters, using 11 species of fish, 3 species of shrimp and 2 species of crabs. I did not test recapture rates in mangrove prop root habitats due to the limited number of sites available and because I assumed recapture rates would be at least as high as elsewhere since red mangrove substrates are dense peat with a thin sediment veneer. This relatively impermeable substrate prevents avoidance by organisms whose escape response is shallow burial in sand or mud. However, organisms that construct semi-permanent burrows such as xanthid crabs were likely underestimated due to potential for retreat into their burrows.

Indices of habitat structure were derived for vegetated habitats. At each mangrove site, the number of prop roots was counted and their intertidal surface area estimated. Total root surface area was estimated by measuring both mid-depth diameter and length from substrate to top of the epiphyte layer of 10 randomly selected roots, calculating the surface area of each based on that of a true cylinder ($\pi \times \text{diameter} \times \text{length}$), then multiplying by the proportional numbers of roots within the sampling site. Numbers of roots were recounted during each visit, but those numbers did not change over the study period. Seagrass standing biomass was estimated from the dry weight of shoots of all species taken from the core at each sampling site. Seagrass dry weights included any attached epiphytes and carbonate materials but excluded roots and rhizomes and drift algae.

A total of 8 drop samples was collected in each habitat each month except September, when 10 drop samples were collected. Salinity and temperature measurements were made within the drop sampler at each site using a temperature-compensated refractometer and a stick thermometer.

Data Analysis.—Relationships between faunal densities or biomasses and habitat variables including water depth, seagrass biomass, and mangrove root number and surface area were explored by simple correlation. Habitat-related density or biomass differences (H_0 : mean densities or biomasses in each habitat were equal) for total fishes, shrimps, and crabs were examined for each sampling period by one-way, model I analysis of variance (ANOVA) with balanced cell sizes. An unbalanced ANOVA design was employed to examine sizes of organisms (H_0 : mean sizes in each habitat were equal) due to unequal numbers of organisms captured and measured. Examination of the distribution of error terms for each major taxon indicated no gross violations of assumed normality, as indicated by the Shapiro-Wilk test statistic (Shapiro and Wilk, 1965). Positive relationships between the means and variances of fish densities and of fish, shrimp and crab biomasses were detected, thus $\log(x + 1)$ -transformation was used to successfully achieve homogeneity of variances. No relationships between means and variances were detected for shrimp and crab densities or for organism lengths, thus untransformed data were analyzed. Tabular data are untransformed means, but ANOVA and multiple comparison results are from transformed data where applicable. Multiple comparison of treatment means employed Ryan's Q test for stepwise unplanned comparisons of density or biomass and Fisher's LSD (least square difference) for size comparisons (Day and Quinn, 1989). All analyses were conducted using SAS software programs (SAS Institute Inc., 1985).

RESULTS

Physical Characteristics.—Water temperature and salinity varied on a seasonal basis as expected from previous studies (Table 1). Salinities were lowest in September (31–33‰) and relatively high (35–37‰) during other sampling months. No consistent differences in salinities or temperatures among habitats were noted, although temperatures were cooler in seagrasses in most months. Water depths at times of sampling were consistently greatest in open water habitats and were usually significantly lower in mangrove habitats than elsewhere.

Mangrove root surface areas varied almost threefold among sampling sites (9,271 to 26,675 cm²), while the number of roots enclosed ranged from 42 to 68. Although 10 mangrove sites were to be sampled each month, erosion of one site and accumulations of debris in other sites prevented collection at all sites except in September. Numbers of samples collected in other habitats were adjusted to maintain balanced designs each month.

Seagrass habitats were mixed beds dominated by shoal grass with lesser amounts of turtle grass, star grass, and manatee grass. Based on seagrass densities in core samples, above-ground dry biomass was estimated to be 14 g·m⁻² in July, 18 g·m⁻² in September, 5 g·m⁻² in December, and 9 g·m⁻² in April.

Faunal Densities.—Quarterly densities of fishes and decapods are given in Tables

Table 1. Water temperature, salinity and depth in flooded mangrove ecosystem habitats in Rookery Bay, Florida, given as mean (\pm standard error). N = 8 in July and December 1988 and April 1989, and N = 10 in September 1988. Refractometer failure in December left only one measurement per habitat. In a given month, means indicated with differing letters were significantly different as defined by the Ryan's Q multiple comparison test

Variable	Month	Mangroves	Open water	Seagrasses
Temperature (C)	July	30.3 (0.13)	30.6 (0.15)	31.9 (0.13)a
	September	30.3 (0.32)	29.8 (0.29)	29.0 (0.20)a
	December	19.5 (0.21)ab	19.9 (0.27)a	19.0 (0.09)b
	April	25.1 (0.24)a	26.3 (0.16)b	24.4 (0.21)c
Salinity (‰)	July	35.4 (0.18)	35.8 (0.41)	36.0 (0.00)
	September	33.0 (0.54)	31.5 (0.17)	31.2 (0.20)
	December	35.0 (0.00)	35.0 (0.00)	35.0 (0.00)
	April	36.8 (0.53)	36.9 (0.67)	36.3 (0.45)
Depth (cm)	July	30.9 (3.21)a	70.9 (5.51)b	48.4 (1.75)c
	September	32.3 (2.31)	38.4 (5.20)	31.0 (2.79)
	December	15.0 (2.21)a	57.4 (3.40)	55.8 (3.61)
	April	22.1 (3.26)a	63.8 (5.10)	51.6 (4.88)

2–5. Thirteen taxa of fishes were collected among flooded prop roots and nearly 75% of their numbers were spotfin mojarra (*Eucinostomus argenteus*). Spotfin mojarra was also numerous in open water and seagrass habitats but was not the numerical dominant in those habitats. Yellowfin menhaden (*Brevoortia smithi*), scaled sardine (*Harengula jaguana*) and striped anchovy (*Anchoa hepsetus*) comprised 75% of the fishes collected in open water habitats. All yellowfin menhaden and scaled sardine were collected in April. In sum, 41 taxa of fishes were recorded from open water sampling sites. The most abundant fish collected over seagrass beds was bay anchovy (*Anchoa mitchilli*; 36% of those captured), followed by spotfin mojarra (13%). A total of 30 taxa of fishes was recorded over seagrass beds. Juvenile fishes of commercial and recreational importance, although never abundant, included lane and gray snappers (*Lutjanus synagris* and *L. griseus*), white and striped mullets (*Mugil curema* and *M. cephalus*), tomtate and white grunt (*Haemulon aurolineatum* and *H. plumieri*), red drum (*Sciaenops ocellatus*), sheepshead (*Archosargus probatocephalus*), and flounder (*Paralichthys* sp.).

Among the decapods, Florida grass shrimp (*Palaemon floridanus*) was the dominant shrimp among prop roots (75% of those collected; Tables 2–5), followed by daggerblade grass shrimp (*Palaemonetes pugio*; 23%). These two species were rare in, or absent from, other habitats. American grass shrimp (*Periclimenes americanus*) was the most numerous shrimp in open water habitats (52% of the catch), followed by green snapping shrimp (*Alpheus normanni*), banded snapping shrimp (*A. armillatus*) and pink shrimp (*Penaeus duorarum*). In seagrass habitats, longtail grass shrimp (*P. longicaudatus*) formed 42% of the catch, followed by pink shrimp, American grass shrimp, and zostera shrimp (*Hippolyte zostericola*). Within the prop root system, crabs such as broadback mud crab (*Eurytium limosum*), green porcelain crab (*Petrolisthes armatus*), and mangrove tree crab (*Aratus pisonii*) were the most abundant among nine taxa collected. *Aratus* is an arboreal crab usually found higher up in mangrove trees, so densities were likely underestimated. In open waters, green porcelain crab and flatback mud crab (*Eurypanopeus depressus*) dominated the 16 taxa recorded with 54% of the number captured. These species and several others are typical of oyster reef habitat, and their abundance at open water sites was likely due to concentrations of shell hash in the sediments

Table 2. Densities (no. per square meter) of mobile macrofauna in flooded mangrove ecosystem habitats in Rookery Bay, Florida, in July 1988. Mean (and standard error) of 8 replicates per habitat

	Fishes				Decapods		
	Mangroves	Open water	Seagrasses		Mangroves	Open water	Seagrasses
<i>Eucinostomus argenteus</i>	6.50 (4.69)	0.54 (0.23)	1.31 (0.31)	<i>Palaemon floridanus</i>	3.23 (0.92)	—	—
<i>Lagodon rhomboides</i>	0.31 (0.15)	—	0.04 (0.04)	<i>Eurytium limosum</i>	1.08 (0.19)	0.19 (0.12)	—
<i>Fundulus grandis</i>	0.04 (0.04)	—	—	<i>Aratus pisonii</i>	0.62 (0.19)	0.12 (0.08)	—
<i>Orthopristis chrysoptera</i>	0.04 (0.04)	—	0.19 (0.12)	<i>Petrolisthes armatus</i>	0.50 (0.19)	2.31 (0.27)	0.04 (0.04)
<i>Bathygobius soporator</i>	0.04 (0.04)	—	—	<i>Palaemonetes pugio</i>	0.42 (0.23)	—	—
<i>Achirus lineatus</i>	—	0.73 (0.23)	0.42 (0.19)	<i>Uca</i> spp.	0.23 (0.19)	—	—
<i>Gobiosoma robustum</i>	—	0.42 (0.15)	0.12 (0.08)	<i>Callinectes sapidus</i>	0.15 (0.08)	0.69 (0.27)	3.23 (1.31)
<i>Symphurus plagiusa</i>	—	0.31 (0.12)	0.54 (0.23)	<i>Penaeus duorarum</i>	0.04 (0.04)	5.19 (1.58)	33.58 (3.38)
<i>Gobiosoma boscii</i>	—	0.19 (0.12)	—	<i>Tozeuma carolinense</i>	0.04 (0.04)	—	4.96 (2.23)
<i>Synodus foetens</i>	—	0.12 (0.08)	0.19 (0.12)	<i>Periclimenes americanus</i>	—	14.77 (5.08)	18.62 (6.00)
<i>Microgobius gulosus</i>	—	0.12 (0.08)	0.12 (0.12)	<i>Alpheus armillatus</i>	—	4.81 (1.08)	—
<i>Anchoa mitchilli</i>	—	0.04 (0.04)	—	<i>Eurypanopeus depressus</i>	—	1.54 (0.73)	0.15 (0.15)
<i>Archosargus probatocephalus</i>	—	0.04 (0.04)	—	<i>Alpheus normanni</i>	—	1.38 (1.38)	9.54 (1.92)
<i>Syngnathus scovelli</i>	—	0.04 (0.04)	0.42 (0.15)	<i>Neopanope packardii</i>	—	0.77 (0.65)	—
Unidentified larvae	—	0.04 (0.04)	—	<i>Pagurus macLaughlinae</i>	—	0.42 (0.35)	0.35 (0.23)
<i>Myrophis punctatus</i>	—	—	0.42 (0.23)	<i>Panopeus occidentalis</i>	—	0.12 (0.12)	0.04 (0.04)
<i>Lutjanus synagris</i>	—	—	0.38 (0.15)	<i>Menippe mercenaria</i>	—	0.04 (0.04)	0.04 (0.04)
<i>Bairdiella chrysoura</i>	—	—	0.15 (0.12)	<i>Pagurus pollicaris</i>	—	0.04 (0.04)	0.15 (0.12)
<i>Hippocampus zosterae</i>	—	—	0.15 (0.15)	<i>Synalpheus townsendi</i>	—	0.04 (0.04)	—
<i>Prionotus carolinus</i>	—	—	0.15 (0.15)	<i>Upogebia affinis</i>	—	0.04 (0.04)	0.04 (0.04)
				<i>Hippolyte zostericola</i>	—	—	24.08 (7.81)
				<i>Portunus ordwayi</i>	—	—	1.73 (0.62)
				<i>Dyspanopeus sayi</i>	—	—	1.38 (0.54)
				<i>Hexapanopeus angustifrons</i>	—	—	1.31 (0.54)
				<i>Pagurus longicarpus</i>	—	—	0.42 (0.42)
				<i>Ambidexter symmetricus</i>	—	—	0.19 (0.12)
				<i>Sicyonia laevigata</i>	—	—	0.15 (0.12)
				<i>Gourretia latispina</i>	—	—	0.04 (0.04)
				<i>Libinia dubia</i>	—	—	0.04 (0.04)
				<i>Metoporphaphis calcarata</i>	—	—	0.04 (0.04)
Total	6.92 (4.85)	2.54 (0.50)	4.38 (0.58)	Total	6.31 (0.85)	32.46 (7.35)	100.08 (13.19)

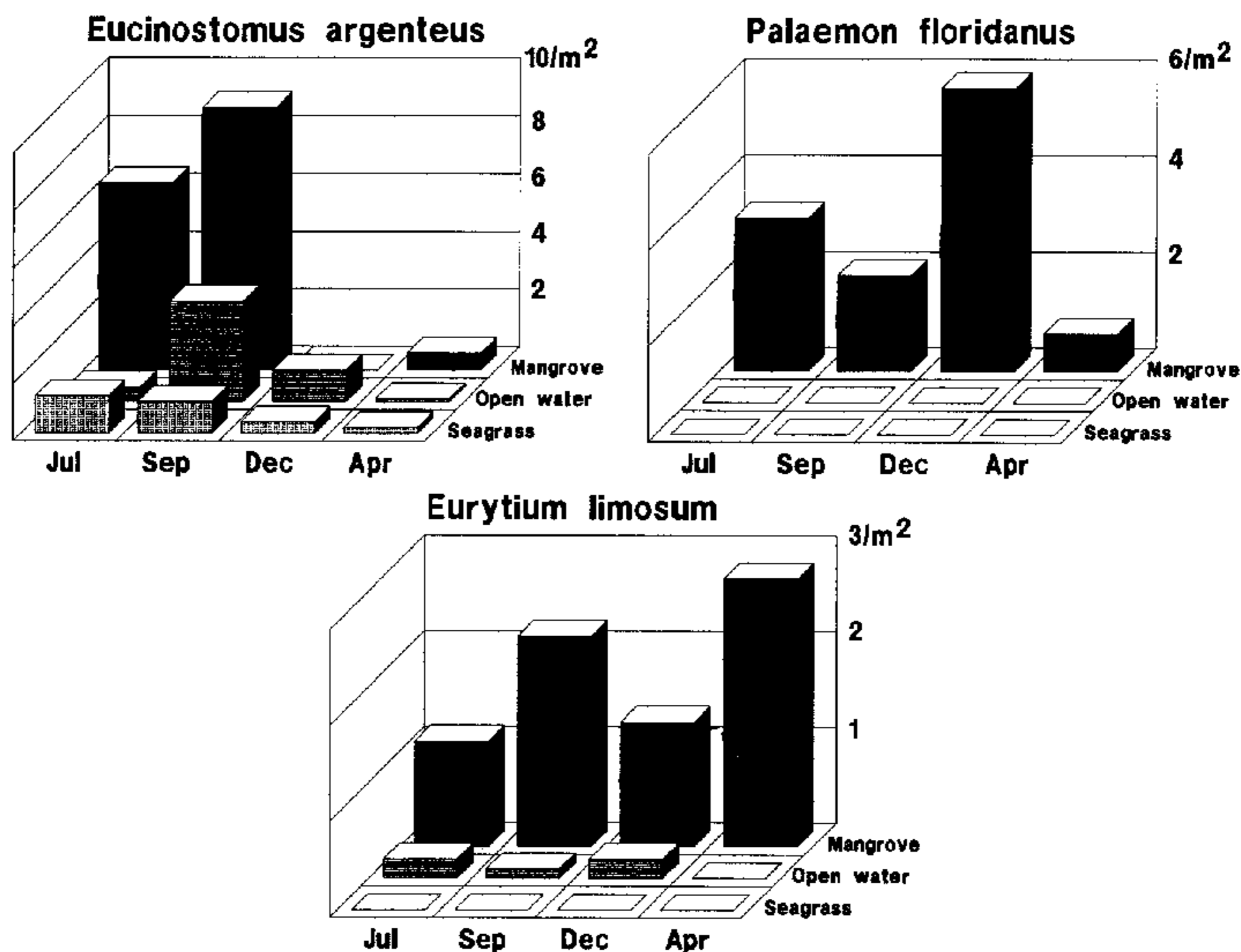


Figure 1. Seasonal densities of dominant species found primarily in mangrove habitats of Rookery Bay.

from barnacles and oysters growing on nearby prop roots. Portunid crabs such as blue crab (*Callinectes sapidus*), iridescent swimming crab (*Portunus gibbesii*), and redhair swimming crab (*P. ordwayi*) were the most abundant taxa in seagrass habitats, together comprising 66% of the crab fauna there. Densities of burrowing shrimps such as *Alpheus*, *Automate*, *Gourretia*, *Synalpheus*, and *Upogebia* and burrowing or cryptic crabs such as *Eurytium* and *Petrolisthes* were likely underestimated.

Certain of these species displayed apparent habitat selection. Spotfin mojarra, Florida grass shrimp, and broadback mud crab were found primarily in mangroves (Fig. 1). Other species, such as pink shrimp, blue crab and longtail grass shrimp, were most dense in seagrasses (Fig. 2). Several dominants were found in two of the three habitats (Fig. 3). These trends will be discussed later.

Seasonality. — Variations in densities of fishes and decapods in each habitat were evident on a seasonal basis. In July, fishes (particularly spotfin mojarra) were most numerous in prop root habitats and least numerous in open waters (Table 2). No species was very numerous in open waters, but densities of lined sole (*Achirus lineatus*), code goby (*Gobiosoma robustum*) and spotfin mojarra were the highest among 11 taxa. Spotfin mojarra was two and one half to three times as abundant as any other fish in seagrass habitats. Among the decapods, Florida grass shrimp and broadback mud crab dominated the mangrove fauna, American grass shrimp and flatback mud crab were most numerous in open water habitats, and pink shrimp and zostera shrimp topped a diverse group in seagrasses. The overall density of decapods was highest in seagrasses and lowest in mangrove prop roots.

September sampling again found spotfin mojarra as the most abundant fish in

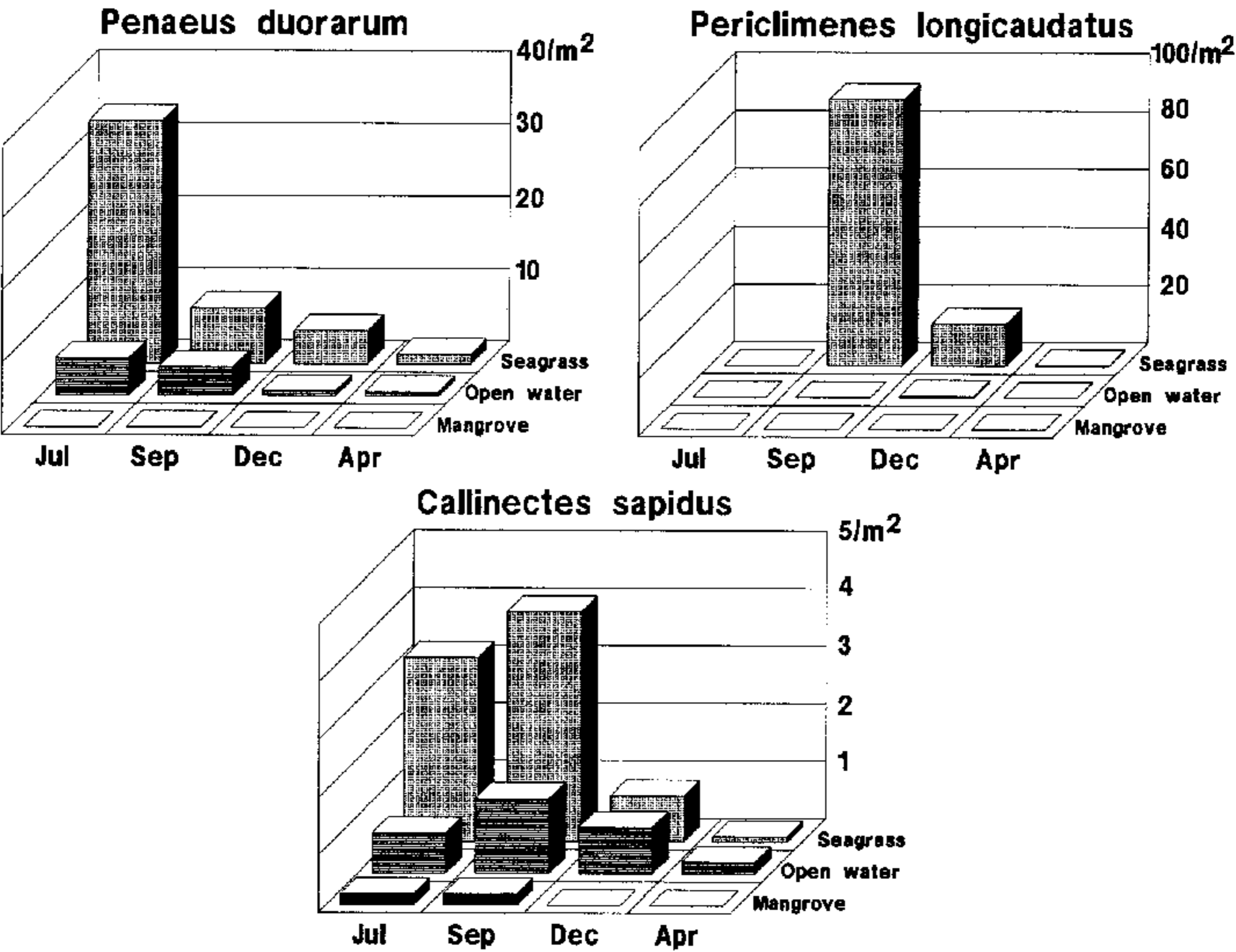


Figure 2. Seasonal densities of dominant species found primarily in seagrass habitats of Rookery Bay.

any habitat, with highest densities among prop roots (Table 3). No other single species was consistently abundant in either open waters or seagrasses, although the overall density of fishes in open waters was close to the density in prop root habitats. As for decapods, broadback mud crab and Florida grass shrimp again dominated the prop root fauna, American grass shrimp and green snapping shrimp were most abundant in open waters, and longtail grass shrimp was eight times as abundant as the next most numerous species in seagrasses.

Silver jenny (*Eucinostomus gula*) replaced spotfin mojarra as the most numerous fish in mangrove habitats in December samples, but it was not found in other habitats (Table 4). Striped anchovy was most numerous (but highly variable) in open waters. Few fishes were encountered over seagrass beds which by that time had exfoliated and were fairly sparse in appearance and above-ground biomass. Fish densities were highest in open waters and similarly low in mangrove and seagrass habitats. Again, Florida grass shrimp was the most abundant shrimp in prop root habitats in December, and these were the highest densities seen all year for this species. Decapods in open waters were characterized by a variety of taxa with roughly similar densities, including snapping shrimps, green porcelain crab, and furrowed mud crab (*Panopeus occidentalis*). In seagrasses, *Periclimenes* spp. and pink shrimp dominated 21 taxa of decapods. Overall decapod densities were still highest in seagrasses, but were similarly low in mangroves and open waters.

Samples collected in April reflected a sparse fish fauna among mangrove roots led once again by spotfin mojarra (Table 5). In open waters, samples were characterized by schools of juvenile yellowfin menhaden and scaled sardine that were patchily distributed, while over seagrasses patchy schools of bay anchovy pre-

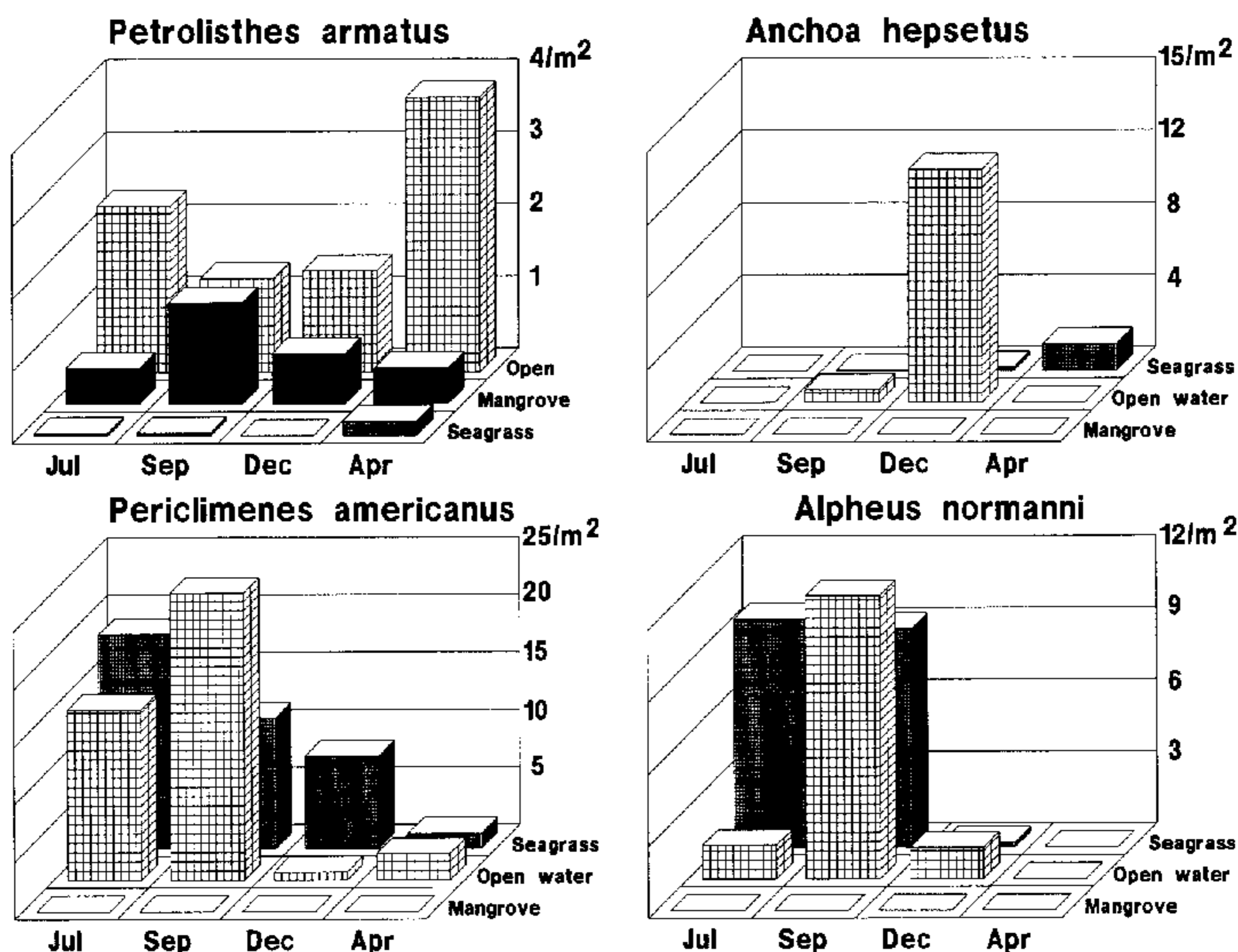


Figure 3. Seasonal densities of dominant species found primarily in open water and seagrass or mangrove habitats of Rookery Bay.

dominated. The large, mixed schools of yellowfin menhaden and scaled sardine (up to 999 in one sample) caused overall fish densities to appear highest in open waters. Decapod densities were led by broadback mud crab and daggerblade grass shrimp in mangroves, by green porcelain crab and banded snapping shrimp in open waters, and by zostera shrimp and iridescent and redhair swimming crabs in seagrasses.

Relation to Habitat Variables.—While habitat-related differences in temperature and salinity exhibited few patterns, water depths were usually least in mangrove habitats and could have influenced relative faunal abundances either by height above the substrate or by volume of water sampled. However, with one exception there were no significant correlations ($P > 0.05$) between water depth and numbers or biomasses of fishes, shrimps and crabs when data were pooled over all habitats in a given month. In April, the number of fishes was significantly correlated with depth ($r = 0.522$, $P < 0.01$, $N = 24$) when large numbers of yellowfin menhaden, scaled sardine and bay anchovy were captured in deeper seagrass and open water sites.

Within-habitat characteristics including water depth, number and surface area of prop roots, and seagrass biomass also were compared with total densities and biomasses of fishes, shrimps, and crabs each month. There were no significant correlations ($P > 0.05$) between organism biomass and habitat characteristics in any month. There were no significant correlations ($P > 0.05$) between organism densities in mangrove habitats and water depth, mangrove root numbers or root surface area in any month. In non-vegetated waters, the only significant corre-

Table 3. Densities of mobile macrofauna (no. per square meter) in flooded mangrove ecosystem habitats in Rookery Bay, Florida, in September 1988. Mean (and standard error) of 10 replicates per habitat

	Fishes				Decapods		
	Mangroves	Open water	Seagrasses		Mangroves	Open water	Seagrasses
<i>Eucinostomus argenteus</i>	9.08 (3.85)	3.50 (0.96)	1.08 (0.27)	<i>Eurytium limosum</i>	2.19 (0.38)	0.08 (0.04)	—
<i>Floridichthys carpio</i>	0.81 (0.50)	—	—	<i>Palaemon floridanus</i>	1.96 (0.65)	—	—
Sciaenidae (larval)	0.31 (0.31)	—	—	<i>Petrolisthes armatus</i>	1.38 (0.35)	1.31 (0.62)	0.04 (0.04)
<i>Lutjanus griseus</i>	0.27 (0.12)	0.08 (0.08)	0.12 (0.08)	<i>Aratus pisonii</i>	0.85 (0.50)	0.04 (0.04)	—
<i>Poecilia latipinna</i>	0.27 (0.15)	—	—	<i>Palaemonetes pugio</i>	0.58 (0.27)	—	—
<i>Bathygobius soporator</i>	0.12 (0.08)	—	—	<i>Callinectes sapidus</i>	0.15 (0.08)	1.27 (0.65)	3.96 (0.89)
<i>Lagodon rhomboides</i>	0.12 (0.08)	0.12 (0.08)	0.04 (0.04)	<i>Sesarma reticulatum</i>	0.15 (0.15)	—	—
Pomadasyidae (larval)	0.12 (0.12)	0.04 (0.04)	—	Xanthidae (unidentified)	0.15 (0.12)	0.04 (0.04)	0.08 (0.08)
<i>Sphyræna guachancho</i>	0.04 (0.04)	0.04 (0.04)	—	<i>Dyspanopeus sayi</i>	0.12 (0.08)	0.46 (0.23)	0.69 (0.23)
<i>Anchoa mitchilli</i>	—	1.92 (1.85)	0.04 (0.04)	<i>Uca</i> sp.	0.12 (0.12)	—	—
<i>Gobiosoma robustum</i>	—	1.50 (0.50)	0.42 (0.15)	<i>Penaeus duorarum</i>	0.08 (0.08)	4.04 (0.73)	7.81 (0.81)
<i>Achirus lineatus</i>	—	1.04 (0.31)	0.12 (0.08)	<i>Periclimenes longicaudatus</i>	0.04 (0.04)	—	92.12 (24.69)
<i>Anchoa hepsetus</i>	—	0.69 (0.46)	0.04 (0.04)	<i>Periclimenes americanus</i>	—	25.54 (8.42)	11.27 (3.58)
<i>Symphurus plagiosa</i>	—	0.31 (0.12)	0.92 (0.27)	<i>Alpheus normanni</i>	—	11.81 (5.92)	9.08 (1.50)
<i>Lutjanus synagris</i>	—	0.15 (0.08)	0.46 (0.15)	<i>Alpheus armillatus</i>	—	1.54 (0.65)	—
<i>Pontinus longispinus</i>	—	0.12 (0.08)	0.04 (0.04)	<i>Panopeus occidentalis</i>	—	0.77 (0.42)	—
<i>Synodus foetens</i>	—	0.08 (0.04)	0.08 (0.04)	<i>Neopanope packardii</i>	—	0.73 (0.50)	0.58 (0.23)
<i>Gunterichthys longipennis</i>	—	0.15 (0.15)	—	<i>Eurypanopeus depressus</i>	—	0.42 (0.19)	—
<i>Haemulon aurolineatum</i>	—	0.15 (0.15)	0.23 (0.12)	<i>Hippolyte zostericola</i>	—	0.27 (0.27)	5.46 (1.35)
<i>Haemulon plumieri</i>	—	0.04 (0.04)	—	<i>Sicyonia laevigata</i>	—	0.15 (0.12)	—
<i>Hypsoblennius hentzi</i>	—	0.04 (0.04)	—	<i>Portunus ordwayi</i>	—	0.12 (0.08)	0.19 (0.15)
<i>Microgobius gulosus</i>	—	0.04 (0.04)	0.04 (0.04)	<i>Menippe mercenaria</i>	—	0.08 (0.04)	—
<i>Prionotus scitulus</i>	—	0.04 (0.04)	—	<i>Pagurus maclaughlinae</i>	—	0.08 (0.04)	0.96 (0.38)
<i>Prionotus tribulus</i>	—	0.04 (0.04)	—	<i>Tozeuma carolinense</i>	—	0.08 (0.08)	6.62 (1.42)
<i>Serraniculus pumilio</i>	—	0.04 (0.04)	—	<i>Pagurus pollicaris</i>	—	0.04 (0.04)	0.19 (0.12)
<i>Syngnathus louisianae</i>	—	0.04 (0.04)	0.04 (0.04)	<i>Leander tenuicornis</i>	—	—	7.00 (2.88)
Unidentified larvae	—	0.04 (0.04)	0.08 (0.04)	<i>Latreutes fucorum</i>	—	—	1.85 (0.65)
<i>Bairdiella chrysoura</i>	—	—	0.23 (0.23)	<i>Latreutes parvulus</i>	—	—	0.42 (0.35)
<i>Gobiosoma boscii</i>	—	—	0.08 (0.08)	<i>Pagurus longicarpus</i>	—	—	0.31 (0.19)
<i>Myrophis punctatus</i>	—	—	0.08 (0.04)	<i>Ambidexter symmetricus</i>	—	—	0.12 (0.08)
<i>Branchiostoma floridae</i>	—	—	0.04 (0.04)	<i>Ogyrides alphaerostris</i>	—	—	0.12 (0.08)
<i>Cynoscion nebulosus</i>	—	—	0.04 (0.04)	<i>Libinia dubia</i>	—	—	0.08 (0.04)
<i>Hippocampus zosterae</i>	—	—	0.04 (0.04)	<i>Polyonyx gibbesi</i>	—	—	0.04 (0.04)
<i>Prionotus carolinus</i>	—	—	0.04 (0.04)	<i>Sicyonia typica</i>	—	—	0.04 (0.04)
Total	11.12 (3.92)	9.96 (1.77)	4.62 (0.58)	Total	7.77 (0.85)	48.85 (14.27)	149.04 (28.88)

Table 4. Densities of mobile macrofauna (no. per square meter) in flooded mangrove ecosystem habitats in Rookery Bay, Florida, in December 1988. Mean (and standard error) of 8 replicates per habitat

	Fishes				Decapods		
	Mangroves	Open water	Seagrasses		Mangroves	Open water	Seagrasses
<i>Eucinostomus gula</i>	1.35 (1.15)	—	—	<i>Palaemon floridanus</i>	5.92 (1.38)	—	—
<i>Poecilia latipinna</i>	0.58 (0.54)	—	—	<i>Eurytium limosum</i>	1.27 (0.27)	0.15 (0.12)	—
<i>Fundulus confluentus</i>	0.54 (0.23)	—	—	<i>Palaemonetes pugio</i>	0.77 (0.65)	—	0.04 (0.04)
Unidentified fish (damaged)	0.12 (0.08)	—	—	<i>Petrolisthes armatus</i>	0.69 (0.19)	1.27 (0.73)	—
<i>Bathygobius soporator</i>	0.04 (0.04)	—	—	<i>Aratus pisonii</i>	0.42 (0.23)	—	—
<i>Lutjanus griseus</i>	0.04 (0.04)	0.04 (0.04)	—	Xanthidae (larval)	0.12 (0.12)	0.04 (0.04)	—
<i>Anchoa hepsetus</i>	—	12.88 (9.38)	0.19 (0.15)	<i>Uca</i> sp.	0.04 (0.04)	—	—
<i>Eucinostomus argenteus</i>	—	1.08 (0.38)	0.38 (0.12)	<i>Alpheus armillatus</i>	—	1.96 (0.65)	0.04 (0.04)
<i>Gobionellus boleosoma</i>	—	0.58 (0.58)	—	<i>Alpheus normanni</i>	—	1.35 (0.93)	0.23 (0.15)
<i>Gobiosoma robustum</i>	—	0.54 (0.42)	0.35 (0.15)	<i>Panopeus occidentalis</i>	—	1.35 (0.42)	0.04 (0.04)
<i>Lutjanus synagris</i>	—	0.23 (0.12)	—	<i>Callinectes sapidus</i>	—	0.81 (0.42)	0.81 (0.19)
<i>Achirus lineatus</i>	—	0.15 (0.08)	—	<i>Penaeus duorarum</i>	—	0.73 (0.19)	4.73 (1.46)
<i>Anchoa mitchilli</i>	—	0.12 (0.12)	—	<i>Periclimenes americanus</i>	—	0.73 (0.38)	8.00 (3.15)
<i>Etropus crossotus</i>	—	0.04 (0.04)	—	<i>Periclimenes longicaudatus</i>	—	0.58 (0.42)	14.73 (6.23)
<i>Gunterichthys longipenis</i>	—	0.04 (0.04)	—	<i>Neopanope packardii</i>	—	0.42 (0.23)	0.19 (0.15)
<i>Haemulon plumieri</i>	—	0.04 (0.04)	—	<i>Leander tenuicornis</i>	—	0.23 (0.15)	0.15 (0.08)
<i>Mugil cephalus</i>	—	0.04 (0.04)	—	<i>Thor dobkini</i>	—	0.23 (0.19)	—
<i>Prionotus tribulus</i>	—	0.04 (0.04)	—	<i>Eurypanopeus depressus</i>	—	0.19 (0.12)	—
<i>Symphurus plagiatus</i>	—	0.04 (0.04)	0.15 (0.08)	<i>Sicyonia laevigata</i>	—	0.19 (0.15)	—
<i>Synodus foetens</i>	—	0.04 (0.04)	0.15 (0.08)	<i>Hippolyte zostericola</i>	—	0.12 (0.08)	2.81 (1.42)
<i>Hippocampus zosterae</i>	—	—	0.04 (0.04)	<i>Menippe mercenaria</i>	—	0.12 (0.08)	—
<i>Microgobius gulosus</i>	—	—	0.15 (0.08)	<i>Panopeus harttii</i>	—	0.12 (0.12)	—
Unidentified larvae	—	—	0.15 (0.12)	<i>Ambidexter symmetricus</i>	—	0.04 (0.04)	0.73 (0.31)
				<i>Callinectes similis</i>	—	0.04 (0.04)	—
				<i>Pagurus macLaughlinae</i>	—	0.04 (0.04)	0.12 (0.12)
				<i>Synalpheus townsendi</i>	—	0.04 (0.04)	—
				<i>Portunus gibbesii</i>	—	—	1.38 (0.38)
				<i>Latreutes parvulus</i>	—	—	0.62 (0.38)
				<i>Tozeuma carolinense</i>	—	—	0.54 (0.19)
				<i>Latreutes fucorum</i>	—	—	0.15 (0.15)
				<i>Libinia dubia</i>	—	—	0.04 (0.04)
				<i>Ogyripdes alphaerostris</i>	—	—	0.04 (0.04)
				<i>Pinnixa retinens</i>	—	—	0.04 (0.04)
Total	2.65 (1.35)	15.92 (9.50)	1.54 (0.31)	Total	9.19 (1.23)	10.73 (2.19)	35.38 (11.92)

Table 5. Densities of mobile macrofauna (no. per square meter) in flooded mangrove ecosystem habitats in Rookery Bay, Florida, in April 1989. Mean (and standard error) of 8 replicates per habitat

	Fishes				Decapods		
	Mangroves	Open water	Seagrasses		Mangroves	Open water	Seagrasses
<i>Eucinostomus argenteus</i>	0.62 (0.19)	0.12 (0.12)	0.15 (0.15)	<i>Eurytium limosum</i>	2.81 (0.46)	—	—
<i>Lagodon rhomboides</i>	0.31 (0.15)	0.12 (0.08)	0.31 (0.12)	<i>Palaemonetes pugio</i>	1.85 (1.85)	—	—
<i>Floridichthys carpio</i>	0.15 (0.12)	—	—	<i>Palaemon floridanus</i>	0.77 (0.42)	—	—
<i>Bathygobius soporator</i>	0.12 (0.08)	0.12 (0.08)	—	<i>Petrolisthes armatus</i>	0.54 (0.23)	4.04 (1.42)	0.15 (0.12)
<i>Eucinostomus gula</i>	0.04 (0.04)	—	—	<i>Aratus pisonii</i>	0.38 (0.23)	—	—
<i>Lutjanus griseus</i>	0.04 (0.04)	—	—	<i>Periclimenes longicaudatus</i>	0.04 (0.04)	—	0.35 (0.23)
<i>Poecilia latipinna</i>	0.04 (0.04)	—	—	<i>Sesarma curacaoense</i>	0.04 (0.04)	—	—
Unidentified larvae	0.04 (0.04)	0.31 (0.12)	0.23 (0.12)	<i>Alpheus armillatus</i>	—	5.23 (1.89)	—
<i>Brevoortia smithi</i>	—	52.40 (92.99)	—	<i>Eurypanopeus depressus</i>	—	2.42 (1.08)	—
<i>Harengula jaguana</i>	—	36.25 (60.26)	—	<i>Periclimenes americanus</i>	—	2.27 (0.73)	1.27 (0.65)
<i>Mugil curema</i>	—	3.69 (3.65)	—	<i>Panopeus occidentalis</i>	—	0.73 (0.38)	—
<i>Membras martinica</i>	—	0.81 (0.62)	—	<i>Neopanope packardii</i>	—	0.58 (0.38)	2.12 (0.73)
<i>Gobiosox strumosus</i>	—	0.35 (0.15)	—	<i>Penaeus duorarum</i>	—	0.58 (0.35)	1.38 (0.35)
<i>Gobiosoma robustum</i>	—	0.31 (0.15)	—	<i>Ambidexter symmetricus</i>	—	0.23 (0.12)	0.38 (0.15)
<i>Achirus lineatus</i>	—	0.23 (0.12)	—	<i>Automate gardineri</i>	—	0.15 (0.15)	—
<i>Gunterichthys longipenis</i>	—	0.23 (0.15)	—	<i>Callinectes sapidus</i>	—	0.15 (0.12)	0.12 (0.08)
<i>Gobionellus boleosoma</i>	—	0.19 (0.12)	0.04 (0.04)	<i>Menippe mercenaria</i>	—	0.12 (0.08)	—
<i>Orthopristis chrysoptera</i>	—	0.15 (0.12)	—	<i>Portunus ordwayi</i>	—	0.12 (0.12)	5.54 (1.23)
<i>Lutjanus synagris</i>	—	0.12 (0.08)	—	<i>Dyspanopeus sayi</i>	—	0.04 (0.04)	1.50 (0.58)
<i>Symphurus plagiusa</i>	—	0.12 (0.12)	0.12 (0.08)	<i>Pagurus maclaughlinae</i>	—	0.04 (0.04)	—
<i>Microgobius gulosus</i>	—	0.04 (0.04)	—	<i>Pagurus pollicaris</i>	—	0.04 (0.04)	0.04 (0.04)
<i>Monacanthus hispidus</i>	—	0.04 (0.04)	—	Portunidae (larval)	—	0.04 (0.04)	—
<i>Opsanus beta</i>	—	0.04 (0.04)	—	<i>Upogebia affinis</i>	—	0.04 (0.04)	—
<i>Pontinus longispinus</i>	—	0.04 (0.04)	—	Xanthidae (larval)	—	0.04 (0.04)	—
<i>Sciaenops ocellatus</i>	—	0.04 (0.04)	—	<i>Hippolyte zostericola</i>	—	—	7.73 (3.35)
<i>Sphoeroides nephelus</i>	—	0.04 (0.04)	—	<i>Portunus gibbesii</i>	—	—	6.50 (1.54)
<i>Synodus foetens</i>	—	0.04 (0.04)	—	<i>Latreutes parvulus</i>	—	—	0.19 (0.19)
<i>Anchoa mitchilli</i>	—	—	8.81 (7.23)	<i>Pagurus longicarpus</i>	—	—	0.15 (0.12)
<i>Anchoa hepsetus</i>	—	—	1.54 (1.00)	<i>Libinia dubia</i>	—	—	0.12 (0.08)
<i>Branchiostoma floridae</i>	—	—	0.50 (0.27)	<i>Synalpheus apioceros</i>	—	—	0.12 (0.12)
<i>Haemulon aurolineatum</i>	—	—	0.38 (0.23)	<i>Tozeuma carolinense</i>	—	—	0.04 (0.04)
<i>Myrophis punctatus</i>	—	—	0.38 (0.12)				
Ophichthidae	—	—	0.19 (0.12)				
<i>Syngnathus scovelli</i>	—	—	0.15 (0.12)				
<i>Paralichthys</i> sp.	—	—	0.04 (0.04)				
<i>Syngnathus louisianae</i>	—	—	0.04 (0.04)				
Total	1.35 (0.31)	95.77 (53.85)	12.85 (7.88)	Total	6.38 (1.96)	16.85 (4.42)	27.62 (4.62)

lations between organism densities and depth were found in December when both fish and shrimp densities were positively correlated with depth ($r = 0.856$ and 0.748 , respectively; $P < 0.05$, $N = 8$). Significant correlations between organism densities and seagrass biomass or depth were only noted in July and December. In July, both shrimp and crab densities were correlated with seagrass biomass ($r = 0.844$ and 0.765 , respectively; $P < 0.05$, $N = 8$), and fish, shrimp, and crab densities were correlated with water depth ($r = 0.720$, 0.839 , and 0.732 , respectively; $P < 0.05$, $N = 8$). However, seagrass biomass was also significantly correlated with water depth ($r = 0.801$, $P < 0.05$, $N = 8$) at this time, preventing a clear interpretation of these trends. In December, fish and crab densities were correlated with seagrass site depth ($r = 0.915$ and 0.853 , respectively; $P < 0.05$, $N = 8$) but not with seagrass biomass.

Habitat-related density and biomass differences for total fishes, shrimps, and crabs were examined on a monthly basis using ANOVA (Table 6). Among-habitat differences in densities or biomasses of major taxa exhibited few patterns. Fish densities were significantly different among habitats only in December and April, when large numbers of striped anchovy, scaled sardine or yellowfin menhaden were captured in open water habitats. Fish biomasses were significantly different only in September, when relatively low biomass was recorded over seagrasses, and in December, when relatively high biomass was collected in open waters. Significant habitat-related differences in shrimp densities were found in all months, with shrimp most numerous in seagrasses, intermediate in open waters, and least numerous among mangrove prop roots. However, shrimp biomasses were significantly different only in July and September when relatively low biomasses were recorded among mangrove prop roots. Crab densities were consistently lower among mangrove prop roots than elsewhere, but significantly so only in July and April. Crab biomasses were only significantly different among habitats in September, when biomass was relatively high around mangrove prop roots.

Habitat-related density differences were also examined by ANOVA for fish and decapod species averaging greater than one individual per sample in any habitat over all samples (Table 7). Although bay anchovy, spotfin mojarra, yellowfin menhaden, scaled sardine, and white mullet appeared to have preferred habitats, differences in densities were not large enough to be significant due to patchy distributions of schools, to variable school sizes, and to seasonal abundance patterns. Striped anchovy, lined sole, and code goby were significantly more abundant in open water habitats than elsewhere, while blackcheek tonguefish (*Symphurus plagiusa*) was significantly more abundant in seagrass beds. Unlike the fishes, the dominant shrimps and crabs all demonstrated significantly higher abundances in at least one habitat. Seven of the 11 most abundant shrimps were associated with seagrasses, two (Florida and daggerblade grass shrimps) were associated with mangroves, while banded snapping shrimp was most abundant in open waters and American grass shrimp was significantly less abundant in mangroves than elsewhere. Six of the 11 crab species were associated with seagrasses, flatback mud crab and green porcelain crab were most abundant in open waters, mangrove tree crab and broadback mud crab were significantly more abundant in mangroves than elsewhere, and Florida grassflat crab (*Neopanope packardii*) was significantly less abundant in mangroves than elsewhere.

Using ANOVA, I compared sizes of at least five individuals of specific fishes, shrimps and crabs occurring in two or three habitats in any given month. No habitat-related size differences were detected for blackcheek tonguefish, lined sole, longtail or American grass shrimps, green snapping shrimp, Florida grassflat crab or Say mud crab (*Dyspanopeus sayi*) in any month tested. Spotfin mojarra were

Table 6. Analysis of variance (ANOVA) comparisons of density and biomass (g, wet weight) per square meter of fishes, shrimps and crabs in flooded mangrove ecosystem habitats in Rookery Bay, Florida. ANOVA $df = 2,21$ in July, December and April, and $df = 2,27$ in September. Means indicated with differing letters in a given month were significantly different (Ryan's Q multiple comparison test)

Taxa	Month	Habitats			ANOVA	
		Mangrove	Open water	Seagrass	F	P
Mean density						
Fishes	July	6.92	2.54	4.38	0.99	0.387
	September	11.12	10.00	4.62	2.36	0.114
	December	2.65	15.92a	1.54	3.98	0.034
	April	1.35	95.73a	12.85	8.84	0.002
Shrimps	July	3.85a	26.35b	96.65c	40.37	0.001
	September	2.65a	43.42b	138.46c	14.13	0.001
	December	6.69	6.19	32.73a	4.91	0.018
	April	2.85	8.50a	11.46a	4.19	0.029
Crabs	July	2.54	6.19a	8.96a	6.96	0.005
	September	5.12	5.42	7.15	1.06	0.360
	December	2.50	4.54	2.65	2.28	0.127
	April	3.77	8.31	16.15a	12.85	0.001
Mean biomass						
Fishes	July	3.54	0.69	2.88	1.45	0.256
	September	10.50	5.23	1.96a	4.20	0.026
	December	1.19	1.77a	0.31	4.42	0.025
	April	1.58	3.88	6.62	1.21	0.319
Shrimps	July	0.42	1.66a	2.50a	14.36	0.001
	September	0.27	1.62a	2.69a	17.97	0.001
	December	0.65	1.00	0.73	0.11	0.894
	April	0.35	1.38	0.35	1.65	0.217
Crabs	July	2.58	1.81	2.62	1.22	0.314
	September	4.96a	1.19	1.50	7.59	0.002
	December	0.85	1.27	0.35	2.54	0.103
	April	3.04	2.46	1.96	1.12	0.345

similarly-sized in all three habitats in July, but in September they were significantly larger in open waters (35 mm; $N = 37$) than in mangrove prop roots (27 mm; $N = 46$) or seagrasses (21 mm; $N = 23$; $F = 8.38$, $P < 0.001$). Pink shrimp did not exhibit size differences in open waters and in seagrasses during July, September or April. However, in December pink shrimp were significantly larger in open waters (36 mm; $N = 14$) than in seagrasses (17 mm; $N = 38$; $F = 45.78$, $P < 0.001$). Blue crabs were similarly-sized in all habitats in July and December, but were significantly larger in open waters (27 mm; $N = 18$) than in seagrasses (12 mm; $N = 44$; $F = 6.61$, $P < 0.001$) during September. Finally, no habitat-related size differences were found for green porcelain crab during December or April, but in September these crabs were significantly larger among prop roots (6 mm; $N = 31$) than in open waters (4 mm; $N = 14$; $F = 6.67$, $P < 0.001$).

DISCUSSION

With the exception of surveys by Yokel (1975), there has been little published research on animal-habitat relationships in Rookery Bay (reviews by Odum et al., 1982; Zieman, 1982; Mahadevan et al., 1984). To the north, Phillips and Springer (1960) and Gunter and Hall (1965) examined the abundance and distribution of fishes and invertebrates in the Caloosahatchee River estuary. Weinstein et al. (1977) described the fishes and invertebrates of Marco Island, a housing

Table 7. Analysis of variance (ANOVA) comparisons of densities (no. per square meter) of relatively abundant fishes, shrimps and crabs in flooded mangrove ecosystem habitats in Rookery Bay, Florida. ANOVA df = 2,31. Means indicated with differing letters were significantly different (Ryan's Q multiple comparison test)

	Mean density			ANOVA	
	Mangrove	Open water	Seagrass	F	P
Fishes					
<i>Anchoa mitchilli</i>	0.00	0.00	2.08	1.99	0.142
<i>Eucinostomus argenteus</i>	4.35	1.42	0.73	2.50	0.087
<i>Brevoortia smithi</i>	0.00	12.33	0.00	2.21	0.116
<i>Harengula jaguana</i>	0.00	8.53	0.00	2.44	0.092
<i>Mugil curema</i>	0.00	0.89	0.00	1.32	0.271
<i>Anchoa hepsetus</i>	0.00	3.23a	0.42	3.12	0.048
<i>Achirus lineatus</i>	0.00	0.58a	0.15	16.89	0.001
<i>Gobiosoma robustum</i>	0.00	0.73a	0.23	17.08	0.001
<i>Symphurus plagiusa</i>	0.00a	0.19b	0.46c	13.58	0.001
Shrimps					
<i>Hippolyte zostericola</i>	0.00	0.12	9.77a	113.18	0.001
<i>Latreutes fucorum</i>	0.00	0.00	0.58a	8.90	0.001
<i>Leander tenuicornis</i>	0.00	0.04	2.08a	9.48	0.001
<i>Periclimenes longicaudatus</i>	0.04	0.15	30.62a	24.43	0.001
<i>Tozeuma carolinense</i>	0.04	0.04	3.23a	33.34	0.001
<i>Alpheus armillatus</i>	0.00	3.70a	0.04	85.05	0.001
<i>Palaemon floridanus</i>	2.92a	0.00	0.00	63.37	0.001
<i>Palaemonetes pugio</i>	0.89a	0.00	0.04	10.29	0.001
<i>Periclimenes americanus</i>	0.00a	11.69	9.85	32.79	0.001
<i>Alpheus normanni</i>	0.00a	4.12b	4.96c	15.56	0.001
<i>Penaeus duorarum</i>	0.04a	2.73b	11.62c	76.08	0.001
Crabs					
<i>Pagurus maclaughlinae</i>	0.00	0.15	0.38a	5.86	0.004
<i>Dyspanopeus sayi</i>	0.04	0.15	0.89a	16.22	0.001
<i>Panopeus occidentalis</i>	0.00	0.04	0.73a	19.27	0.001
<i>Portunus gibbesii</i>	0.00	0.00	1.85a	21.95	0.001
<i>Portunus ordwayi</i>	0.00	0.04	1.77a	18.45	0.001
<i>Eurypanopeus depressus</i>	0.00	1.12a	0.04	22.43	0.001
<i>Aratus pisonii</i>	0.58a	0.04	0.00	20.80	0.001
<i>Eurytium limosum</i>	1.85a	0.12	0.00	185.94	0.001
<i>Neopanope packardii</i>	0.00a	0.62	0.73	7.24	0.001
<i>Callinectes sapidus</i>	0.08a	0.77b	2.15c	19.56	0.001
<i>Petrolisthes armatus</i>	0.81a	2.15b	0.04c	25.10	0.001

development in mangrove habitat just south of Rookery Bay. Farther south, Colby et al. (1985) and Browder et al. (1986) examined the fishes and invertebrates of Faka Union Bay and several adjacent embayments. All of these studies sampled with trawls, but only Yokel compared adjacent habitats.

Yokel (1975) conducted a 26-month trawl survey of fishes and invertebrates in Rookery Bay. Stations located over seagrass beds and near stands of red mangrove yielded higher total catches of trawl-susceptible fishes and invertebrates than open water stations. The most abundant fishes in Yokel's survey were pinfish (*Lagodon rhomboides*; 42% of the total numbers caught) and silver jenny (31%). In my study, these two species represented only 1% each of the total fishes caught. This may be a result of sampling gear but also may be indicative of different rainfall regimes (i.e., Yokel monitored several runoff events that depressed salinities to 0‰, whereas I saw little salinity change) or of long-term changes in the Rookery

Bay system. Small caridean shrimps dominated Yokel's invertebrate catches, with longtail and American grass shrimps, zostera shrimp, and arrow shrimp (*Tozeuma carolinense*) comprising 40% of all invertebrates collected by trawl, while pink shrimp was the third most numerous invertebrate, representing 11% of the catch. These same species were among the most abundant in my samples, but the drop sampler was a more effective means of documenting the relatively high densities of alpheid shrimps in open waters and seagrass beds and of Florida grass shrimp among red mangrove prop roots that were not sampled by trawl.

Several studies conducted in southwest Florida have quantified fish or invertebrate densities in mangrove ecosystem habitats. I was able to compare my data from seagrass habitats with those from quantitative throw-trap surveys by Sogard et al. (1987) and Holmquist et al. (1989) conducted in Florida Bay, part of Everglades National Park. In Rookery Bay seagrasses, bay anchovy, silver jenny, blackcheek tonguefish, and striped anchovy were the most abundant fishes (64% of the total), but these species were either rare or not collected in Florida Bay seagrasses. The dominant fishes recorded by Sogard et al. (1987) included goldspotted killifish (*Floridichthys carpio*, 27%), rainwater killifish (*Lucania parva*, 19%), oyster toadfish (*Opsanus beta*, 16%), and code goby (14%), but these taxa were either relatively low in abundance or absent from Rookery Bay seagrasses. Fish densities in Rookery Bay seagrass habitats were about half the densities in Florida Bay (grand means, $5.8 \text{ fish} \cdot \text{m}^{-2}$ versus $11.0 \text{ fish} \cdot \text{m}^{-2}$, respectively; Sogard et al., 1987).

Longtail and American grass shrimps, zostera shrimp, and pink shrimp were among the dominant shrimp taxa in seagrasses in both Rookery Bay and Florida Bay (Holmquist et al., 1989). One major difference was that the most numerous shrimp in Florida Bay, bryozoan shrimp (*Thor floridanus*), was absent from Rookery Bay (although I collected squat grass shrimp (*T. dobkini*) on rare occasions). Species compositions of the crab faunas were quite dissimilar: *Pagurus maclaughlinae* and Florida grassflat crab were the dominants in Florida Bay, while blue crabs and other portunids were most abundant in Rookery Bay. Decapod densities at Holmquist et al.'s "Gulf" seagrass sites (those most likely to resemble Rookery Bay) averaged $133 \text{ shrimp} \cdot \text{m}^{-2}$ and $12 \text{ crabs} \cdot \text{m}^{-2}$, while in Rookery Bay the overall average densities in seagrass habitats were $74 \text{ shrimp} \cdot \text{m}^{-2}$ and $9 \text{ crabs} \cdot \text{m}^{-2}$.

The only quantitative sampling of fishes in flooded mangroves has been conducted by Thayer et al. (1987) who used block nets and rotenone to estimate fish densities in Florida Bay. Spotfin mojarra dominated Rookery Bay catches (74%) but were relatively sparse (4%) in Florida Bay mangroves. In contrast, Florida Bay mangrove communities were more diverse and were dominated by hardhead silverside (*Atherinomorus stipes*), silver jenny, goldspotted killifish, and rainwater killifish, together comprising 67% of the fishes collected. Fish densities in mangrove habitats were comparable between Rookery Bay (grand mean $5.9 \text{ fish} \cdot \text{m}^{-2}$) and Florida Bay (grand geometric mean, $8.0 \text{ fish} \cdot \text{m}^{-2}$; Thayer et al., 1987).

There have been relatively few studies quantifying densities of macrofauna in mangrove and seagrass habitats outside of Florida. Jamaican red mangroves harbored crabs such as *Aratus*, *Eurytium*, and *Panopeus* at densities of $41 \cdot \text{m}^{-2}$, as determined by a one-time quadrat survey that included digging crabs from burrows and removing them from trees (Warner, 1969). Crab densities in Rookery Bay red mangroves averaged $3.6 \cdot \text{m}^{-2}$ and peaked at $5.1 \cdot \text{m}^{-2}$ in September, but I did not collect above and below the peat surface. Seagrass beds adjacent to red mangroves in the Indian River on the Atlantic coast of Florida supported decapod communities similar in taxa and density ($90 \cdot \text{m}^{-2}$; Gore et al., 1981) to those in Rookery Bay seagrasses ($82 \cdot \text{m}^{-2}$). Bauer (1985a; 1985b) collected similar genera

Table 8. Macrofauna found primarily in a single Rookery Bay habitat, based on capture of at least 10 specimens. Asterisk (*) indicates species recorded as relatively abundant in other Florida habitats, including intertidal marshes, by prior investigators (see text)

	Mangroves	Open water	Seagrasses
Fishes	<i>Eucinostomus gula</i> * <i>Floridichthys carpio</i> * <i>Fundulus confluentus</i> * <i>Poecilia latipinna</i> *	<i>Brevoortia smithi</i> <i>Harengula jaguana</i> <i>Gobionellus boleosoma</i> <i>Membras martinica</i> <i>Mugil curema</i> *	<i>Anchoa mitchilli</i> * <i>Haemulon aurolineatum</i> <i>Myrophis punctatus</i> <i>Syngnathus scovelli</i> *
Shrimps	<i>Palaemon floridanus</i> * <i>Palaemonetes pugio</i> *	<i>Alpheus armillatus</i>	<i>Ambidexter symmetricus</i> <i>Hippolyte zostericola</i> <i>Latreutes fucorum</i> <i>Latreutes parvulus</i> <i>Leander tenuicornis</i> <i>Periclimenes longicaudatus</i> <i>Tozeuma carolinense</i>
Crabs	<i>Aratus pisonii</i> <i>Eurytium limosum</i> *	<i>Eurypanopeus depressus</i> <i>Panopeus occidentalis</i>	<i>Hexapanopeus angustifrons</i> <i>Pagurus longicarpus</i> <i>Portunus gibbesii</i> * <i>Portunus ordwayi</i>

but much lower densities of shrimps ($18 \cdot \text{m}^{-2}$) from turtle grass and manatee grass beds in Puerto Rico. Morton (1990) recently provided the second quantitative analysis of fish abundance in flooded mangroves (*Avicennia marina*) from Queensland, Australia. By block-netting a known area beneath the canopy at high tide and returning at low tide, Morton documented one of the highest standing crops of fishes in any estuarine habitat (13-month average of $25.3 \text{ g} \cdot \text{m}^{-2}$). The average number of fishes caught was low ($0.27 \cdot \text{m}^{-2}$) because a large mesh (18 mm) was employed. In Rookery Bay, average fish biomass was about $4 \text{ g} \cdot \text{m}^{-2}$. Robertson and Duke (1987) compared relative abundances of fishes and crustaceans caught by seine in adjoining mangrove creeks, seagrasses and sand banks at several sites in Queensland, Australia as well. Creeks next to mangroves averaged 6 times the number of fishes as adjacent seagrass habitats and 23 times the fishes as nearby sand banks. Decapods were more abundant in seagrasses (1.2 times) and sand banks (4.4 times) than in mangrove creeks. Densities of fishes in my open water sites were 5.6 times those in seagrass sites, similar to the relative abundances observed by Robertson and Duke, but decapods in Rookery Bay were 2.9 times as abundant in seagrasses as in open waters.

In addition to the more numerous species already discussed, a number of species appeared more abundant in one Rookery Bay habitat over others (Table 8), giving the impression of distinct animal communities. Most of these fishes and several decapods, however, have been recorded as relatively numerous in other habitats (Dugan and Livingston, 1982; Gore et al., 1981; Sogard et al., 1987; Subrahmanyam and Coultas, 1980; Thayer et al., 1987; Weinstein et al., 1977). Nocturnal collecting could also change apparent habitat specificity, more so for decapods that burrow during the day than for fishes (Bauer, 1985a; Sogard et al., 1987). Perhaps the only organisms truly restricted to certain habitats are the arboreal mangrove tree crab and the small caridean shrimps typical of seagrasses. The distributions of those shrimps could be equally influenced by competitive or predatory interactions as by some habitat feature. There is a relative lack of information on crab distributions, and there is a need to test habitat specificity of congeners such as *Periclimenes longicaudatus* and *P. americanus* or *Alpheus armillatus* and *A. normanni*. The influences of such factors as food availability

and predation on the distributions of organisms among Rookery Bay habitats also await investigation.

At certain times of the year, intertidal red mangrove habitats supported macrofaunal densities similar to those in adjacent seagrass and open water habitats. Species diversity, however, was usually much lower. Organisms such as spotfin mojarra, pinfish, gray snapper, and green porcelain crab were able to exploit flooded red mangroves along with other habitats, while other abundant species such as yellowfin menhaden, scaled sardine, anchovies, pink shrimp, snapping shrimp, and portunid crabs rarely moved into the prop roots. Still others (*Eurytium*, *Aratus*, *Uca*, *Sesarma*) were red mangrove residents that occasionally moved out of the prop roots to the adjacent non-vegetated areas. Intertidal vegetated habitats are thought to provide greater densities of food and greater degrees of protection than non-vegetated habitats and thus should attract mobile organisms as these habitats become available. Comparative analyses have been conducted for seagrass versus non-vegetated habitats. Potential prey densities (infauna, epifauna, zooplankton) are higher in seagrass habitats than in open waters (Virnstein et al., 1983; Lewis, 1984; Robertson et al., 1988), and seagrasses may offer greater degrees of protection from predators (Wilcox et al., 1975; Nelson, 1979; Heck and Thoman, 1981, 1984; Wilson et al., 1987; Diehl, 1988). Mangroves may not provide the same functions as seagrasses, although research in these areas is relatively limited. Zooplankton densities were lower in flooded mangroves than over seagrass beds or in open waters (Robertson et al., 1988). Comparisons of benthic infauna and epifauna indicated densities within mangroves can be either higher (Dye, 1983; Hodda and Nicholas, 1985; Wells, 1986) or lower (Kolehmainen and Hildner, 1975; Wells, 1983; Alongi, 1987) than in adjoining mud flats or seagrass beds. Although I found little evidence for this, mobile invertebrates such as penaeid shrimp and portunid crabs do move into flooded mangroves (Hill et al., 1982; Robertson, 1988) and may be major predators on the benthos or resident macrofauna (Wilson, 1989). Larger fishes also forage among the prop roots (Hettler, 1989). However, comparative analyses of predation efficiency in flooded mangroves versus open waters or seagrasses are lacking.

ACKNOWLEDGMENTS

This research would not have been completed without the field and laboratory assistance of the following good-natured scientists: Dr. J. Nance, E. Martinez, F. Patella, T. Czapla, M. Pattillo, R. Haneke, L. Scott-Denton, S. Ireland, K. Jaynes, and D. Emiliani (all National Marine Fisheries Service) and Dr. C. McIvor (U.S. Fish and Wildlife Service). Special recognition goes to S. Bertone (Florida Department of Natural Resources) for his long hours assisting each trip. My thanks also to Dr. K. Thoemke, Director of the Rookery Bay National Estuarine Research Reserve at the time of my research, for allowing us to use space and vessels. I appreciate the work of M. Dentzau (Florida Department of Environmental Regulation) in securing a permit for sampling in the mangroves. Identities of small *Membras*, *Brevoortia*, *Harengula*, *Gobiesox*, and *Anchoa* were provided by Dr. M. Leiby (Florida Department of Natural Resources). Constructive reviews of this manuscript were provided Drs. T. Minello and E. Klima, by Z. Zein-Eldin and by two anonymous referees.

LITERATURE CITED

- Alongi, D. M. 1987. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. *Mar. Ecol. Prog. Ser.* 40: 103-114.
- Bauer, R. T. 1985a. Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico. *Bull. Mar. Sci.* 36: 150-162.
- . 1985b. Penaeoid shrimp fauna from tropical seagrass meadows: species composition, diurnal, and seasonal variation in abundance. *Proc. Biol. Soc. Wash.* 98: 177-190.
- Browder, J. A., A. Dragovitch, J. Tashiro, E. Coleman-Duffie, C. Foltz and J. Zweiffel. 1986. Comparison of biological abundances in three adjacent bay systems downstream from the Golden Gates Estates canal system. NOAA Tech. Memo. NMFS-SEFC-185. 96 pp.

- Chapman, V. J. 1977. Introduction. Pages 1–29 in V. J. Chapman, ed. *Ecosystems of the world 1. Wet coastal ecosystems*. Elsevier Scientific Publ. Co., Amsterdam.
- Colby, D. R., G. W. Thayer, W. F. Hettler and D. S. Peters. 1985. A comparison of forage fish communities in relation to habitat parameters in Faka Union Bay, Florida, and eight collateral bays during the wet season. NOAA Tech. Memo. NMFS-SEFC-162.
- Day, R. W. and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59: 433–463.
- Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* 53: 207–214.
- Dugan, P. J. and R. J. Livingston. 1982. Long-term variation of macroinvertebrate assemblages in Apalachee Bay, Florida. *Estuar. Coast. Shelf Sci.* 14: 391–403.
- Dye, A. H. 1983. Composition and seasonal fluctuations of meiofauna in a southern African mangrove estuary. *Mar. Biol.* 73: 165–170.
- Gore, R. H., E. E. Gallaher, L. E. Scotto and K. A. Wilson. 1981. Studies on decapod Crustacea from the Indian River region of Florida. XI. Community composition, structure, biomass and species-areal relationships of seagrass and drift algae-associated macrocrustaceans. *Estuar. Coast. Shelf Sci.* 12: 485–508.
- Gunter, G. and G. E. Hall. 1965. A biological investigation of the Caloosahatchee estuary of Florida. *Gulf Res. Rept.* 2(1): 1–72.
- Heck, K. L., Jr. and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53: 125–134.
- and ———. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7: 70–92.
- Hettler, W. F., Jr. 1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bull. Mar. Sci.* 44: 155–162.
- Hill, B. J., M. J. Williams and P. Dutton. 1982. Distribution of juvenile, subadult and adult *Scylla serrata* (Crustacea: Portunidae) on tidal flats in Australia. *Mar. Biol.* 69: 117–120.
- Hodda, M. and W. L. Nicholas. 1985. Meiofauna associated with mangroves in the Hunter River estuary and Fullerton Cove, south-eastern Australia. *Aust. J. Mar. Freshw. Res.* 36: 41–50.
- Holmquist, J. G., G. V. N. Powell and S. M. Sogard. 1989. Decapod and stomatopod communities of seagrass-covered mud banks in Florida Bay: inter- and intra-bank heterogeneity with special reference to isolated subenvironments. *Bull. Mar. Sci.* 44: 251–262.
- Kolehmainen, S. E. and W. K. Hildner. 1975. Zonation of organisms in Puerto Rican red mangrove (*Rhizophora mangle* L.) swamps. Pages 357–369 in G. E. Walsh, S. C. Snedaker and H. J. Teas, eds. *Proceedings of the International Symposium on Biology and Management of Mangroves*. Univ. of Florida, Inst. of Food Agric. Sciences, Gainesville, Florida.
- Lewis, F. G., III. 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. *Mar. Ecol. Prog. Ser.* 19: 101–113.
- Lewis, R. R., R. G. Gilmore, Jr., D. W. Crews and W. E. Odum. 1985. Mangrove habitat and fishery resources of Florida. Pages 281–336 in W. Seaman, Jr., ed. *Florida aquatic habitat and fishery resources*. Florida Chapter of the American Fisheries Society, Kissimmee, Florida.
- Mahadevan, S., J. Sprinkel, D. Heatwole and D. H. Wooding. 1984. Bibliography of benthic studies in the coastal and estuarine areas of Florida. Florida Sea Grant Publ. SGR-66. 576 pp.
- Martosubroto, P. and N. Naamin. 1977. Relationship between tidal forests (mangroves) and commercial shrimp production in Indonesia. *Mar. Res. Indonesia* 18: 81–86.
- Minello, T. J. and R. J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.* 72: 211–231.
- and ———. 1985. Differential selection for vegetative structure between juvenile brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*), and implications in predator-prey relationships. *Estuar. Coast. Shelf Sci.* 20: 707–716.
- Morton, R. M. 1990. Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. *Mar. Biol.* 105: 385–394.
- Nelson, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.* 38: 225–245.
- Odum, W. E., C. C. McIvor and T. G. Smith. 1982. The Florida mangrove zone: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-82/24. 144 pp.
- Phillips, R. C. and V. G. Springer. 1960. A report on the hydrography, marine plants, and fishes of the Caloosahatchee River, Lee County, Florida. Florida Board of Conservation, Spec. Sci. Rept. No. 5. 34 pp.
- Robertson, A. I. 1988. Abundance, diet and predators of juvenile banana prawns, *Penaeus merguensis*, in a tropical mangrove estuary. *Aust. J. Mar. Freshw. Res.* 39: 467–478.
- , P. Dixon and P. A. Daniel. 1988. Zooplankton dynamics in mangrove and other nearshore habitats in tropical Australia. *Mar. Ecol. Prog. Ser.* 43: 139–150.

- and N. C. Duke. 1987. Mangroves as nursery sites: comparisons of the abundance of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* 96: 193–206.
- Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada, 4th ed. Amer. Fish. Soc. Spec. Publ. 12. 174 pp.
- Rookery Bay National Estuarine Research Reserve. 1986. Management plan. Florida Dep. Nat. Res., Rookery Bay Nat. Est. Res. Reserve, Naples, Florida. 62 pp.
- Rozas, L. P. and W. E. Odum. 1987. Use of tidal freshwater marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. *Estuaries* 10: 36–43.
- SAS Institute Inc. 1985. SAS Procedures guide and SAS/STAT guide for personal computers, Version 6 Ed. SAS Institute Inc., Cary, North Carolina. 373 pp. and 378 pp.
- Shapiro, S. S. and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591–611.
- Sherrod, C. L. and C. McMillan. 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contrib. Mar. Sci.* 28: 129–140.
- Sogard, S. M., G. V. N. Powell and J. G. Holmquist. 1987. Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. *Mar. Ecol. Progr. Ser.* 40: 25–39.
- Subrahmanyam, C. B. and C. L. Coultas. 1980. Studies on the animal communities in two north Florida salt marshes. Part III. Seasonal fluctuations of fish and macroinvertebrates. *Bull. Mar. Sci.* 30: 790–818.
- Thayer, G. W., D. R. Colby and W. F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. *Mar. Ecol. Progr. Ser.* 35: 25–38.
- Tilmant, J. T. 1989. A history and an overview of recent trends in the fisheries of Florida Bay. *Bull. Mar. Sci.* 44: 3–33.
- Turner, R. E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. *Trans. Amer. Fish. Soc.* 106: 411–416.
- Virnstien, R. W., P. S. Mikkelsen, K. D. Cairns and M. A. Capone. 1983. Seagrass beds versus sand bottoms: the trophic importance of their associated benthic invertebrates. *Florida Sci.* 46: 363–381.
- Warner, G. F. 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. *J. Anim. Ecol.* 38: 379–389.
- Weinstein, M. P., C. M. Hackney and J. C. Kinch. 1977. The Marco Island estuary: a summary of physicochemical and biological parameters. *Florida Sci.* 40: 97–124.
- Wells, F. E. 1983. An analysis of marine invertebrate distributions in a mangrove swamp in north-western Australia. *Bull. Mar. Sci.* 33: 736–744.
- . 1986. Distribution of molluscs across a pneumatophore boundary in a small bay in north-western Australia. *J. Moll. Stud.* 52: 83–90.
- Wilcox, L. V., Jr., T. G. Yocom, R. C. Goodrich and A. M. Forbes. 1975. Ecology of mangroves in the Jewfish Chain, Exuma, Bahamas. Pages 305–343 in G. E. Walsh, S. C. Snedaker and H. J. Teas, eds. *Proceedings of the International Symposium on Biology and Management of Mangroves*. Univ. of Florida, Inst. Food Agric. Sciences, Gainesville, Florida.
- Williams, A. B., L. G. Abele, D. L. Felder, H. H. Hobbs, Jr., R. B. Manning, P. A. McLaughlin and I. Pérez Farfante. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. Amer. Fish. Soc. Spec. Publ. 17. 277 pp.
- Wilson, K. A. 1989. Ecology of mangrove crabs: predation, physical factors and refuges. *Bull. Mar. Sci.* 44: 263–273.
- , K. L. Heck, Jr. and K. W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fish. Bull. U.S.* 85: 53–58.
- Yokel, B. J. 1975. Rookery Bay land use studies. Environmental planning strategies for the development of a mangrove shoreline. Study No. 5—Estuarine Biology. The Conservation Foundation, Washington, D.C. 112 pp.
- Zieman, J. C. 1982. The ecology of seagrasses of south Florida: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-82/25. 158 pp.
- Zimmerman, R. J. and T. J. Minello. 1984. Densities of *Penaeus aztecus*, *P. setiferus*, and other natant macrofauna in a Texas salt marsh. *Estuaries* 7: 421–433.
- Zimmerman, R. J., T. J. Minello and G. Zamora, Jr. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. *Fishery Bull. U.S.* 82: 325–336.

DATE ACCEPTED: March 12, 1991.

ADDRESS: NOAA/National Marine Fisheries Service, Southeast Fisheries Center, 4700 Avenue U, Galveston, Texas 77551-5997.